tory feeding observations and those of other workers could be artifacts of laboratory starvation.

The limited number of *Calliostoma variegatum* collected was fixed for gut analyses, and only one was observed in the laboratory. *Calliostoma ligatum* feeding behavior was observed both in the laboratory and in the field, but no controlled experiments were run on this species.

RESULTS

a) **Field observations:** Nearly all of the 100+ *Calliostoma annulatum* observed by diving were found actively feeding in beds of campanularid and sertularid hydroids. Close inspection revealed that both hydranths and stems were consumed, and that nudibranch eggs were commonly swallowed along with the hydroids. Clumps of hydroids collected off Eagle Point sometimes contained young *C. annulatum* as small as 3.2 mm in shell height.

During this study, *Calliostoma annulatum* was never found on any part of the kelp *Nereocystis luetkeana,* which is the dominant canopy-forming alga around San Juan Island. This observation contrasts with those of McLean (1962) and Lowry *et al.* (1974) who found *C. annulatum* to be common on the fronds of canopy-forming algae off the coast of California.

Calliostoma ligatum is abundant low in the intertidal zone around San Juan Island, and is found subtidally where its range overlaps that of *C. annulatum. Calliostoma ligatum* was never observed feeding on hydroids in the field, and small numbers of this gastropod were found on the stipes, but not on the fronds, of *Nereocystis.*

b) **Gut content analyses:** The stomachs and intestines of 54 of the 56 *Calliostoma annulatum* examined were nearly filled with hydroid fragments. Although the majority of the remains was of sertularids and campanularids, pieces of gymnoblast stems were also found. Each gut contained various amounts of debris which included sand grains, sponge spicules and diatoms. One gut contained high concentrations of sponge spicules.

Seven of the 8 *Calliostoma variegatum* guts were also filled with hydroids. However, since no hydroids were identified beneath the family level, it is inadvisable to conclude that the diets of *C. annulatum* and *C. variegatum* are identical.

The guts of all intertidal *Calliostoma ligatum* were filled with diatoms, and no hydroid fragments were observed. The gut contents of the 53 subtidal *C. ligatum* (collected from 80 m) consisted mainly of debris composed of sand and unidentified detritus. The few hydroid fragments found could easily have been scraped up along with debris and probably are an insignificant part of the animal's diet.

c) **Laboratory experiments and observations:** There was no apparent difference in feeding behavior between starved and unstarved *Calliostoma annulatum.* When placed in bowls containing the stauromedusan *Haliclystis* sp. all 20 starved and all but one unstarved *C. annulatum* quickly consumed the cnidarian prey. Similar results were obtained using both thecate and athecate hydroids as prey animals. However, when *C. annulatum* was presented with green and brown algae, there was no observable feeding.

During the course of the present study, *Calliostoma annulatum* kept in the laboratory were observed feeding on nudibranch eggs, the anemone *Epiactis prolifera* (Verrill, 1869), the sea pen *Ptilosarcus gurneyi* (Gray), dead chitons, the ectoproct *Membranipora membranacea* (Linnaeus, 1767), and "Alpo" dog food. No large algae were ever consumed, although some scraping of diatom films was noted. *Calliostoma ligatum* also fed on hydroids in the laboratory.

The feeding behavior of *Calliostoma annulatum* was carefully observed. When a hydroid was approached, first contact was made with the tentacles. As the mouth came in contact with the hydroid, the snail's lips would open laterally, and with a quick lunge, the head would move forward while the radula seized the hydroid stem or hydranth. This behavior seemed to be elicited more strongly by contact with hydranths than with stems, especially when athecate hydroids such as *Tubularia marina* (Torrey, 1902) were encountered.

As hydroid stems entered the mouth, they were either pinched off by the jaws or were held while the radula rasped them apart. Observations of *Calliostoma annulatum* consuming ectoprocts indicate that the *Calliostoma* radula is capable of efficient rasping. However, hydroid stem fragments recovered from the guts of *Calliostoma* were often neatly cut into short segments, suggesting that the jaws of this gastropod may be stronger than formerly thought (Clench & Turner, 1960).

Calliostoma annulatum showed more intensified "attack" behavior when attempting to feed on anemones. Upon initial contact with an anemone the gastropod would rear up on its metapodium, expand its lips, and suddenly lunge forward while biting at one of the anemone's tentacles. This behavior was observed repeatedly, and in one case, a dorid nudibranch was attacked in the same manner.

DISCUSSION AND CONCLUSIONS

The data on gut contents presented here show that *Calliostoma annulatum* and *C. variegatum* are at least facultative predators on hydroids. The feeding experiments performed on *C. annulatum* indicate that the laboratory observations of predation on animals other than hydroids are probably not artifacts of starvation. Since the tissue of soft-bodied animals could easily have been missed in the analyses of gut contents it is possible that non-hydroid animal prey may be taken in the field.

It is somewhat perplexing, however, that although *Calliostoma ligatum* fed on hydroids in the laboratory, specimens collected in the field rarely contained more than a few hydroids in their guts. The difference in diet between intertidal and subtidal *C. ligatum* needs further study, and the data available to date do not warrant classification of *C. ligatum* as a carnivore.

The radulae of *Calliostoma annulatum, C. variegatum,* and *C. ligatum* are similar, and all are typical of the genus (Clench & Turner, 1960). The major difference noted between the radulae of the three species was that the first marginal tooth in *C. ligatum* is less well developed than in *C. annulatum* or *C. variegatum.*

Dayton (1973) stressed the point that ecological models should be based on a thorough understanding of relevant natural history, and Sanders (1962) showed that several species of errant polychaetes, long assumed to be strictly carnivorous, were actually detritus-feeding omnivores. The present study further emphasizes the danger inherent in making assumptions about trophic position in the absence of specific feeding data.

Further literature search would doubtless reveal additional documentation of carnivores among the Archaeogastropoda. However, a more productive approach to the problem would be a reevaluation of feeding in the Archaeogastropoda based on extensive and detailed field observations.

SUMMARY

Gut content analyses supplemented by laboratory and field observations have shown that *Calliostoma annulatum* [Lightfoot, 1786] and *C. variegatum* (Carpenter, 1864) feed extensively on thecate and athecate hydroids. Laboratory observations suggest that *C. annulatum* may feed on additional animal prey. A third species of *Calliostoma, C. ligatum* (Gould, 1846), feeds on diatoms in the intertidal zone and on detritus subtidally.

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